THE TAXONOMIC STATUS OF *OXYPOLIS GREENMANII* (APIACEAE)

WALTER S. JUDD

Oxypolis greenmanii was first described by Mathias and Constance (1942), although it had been collected much earlier (see *Chapman*, Aug. 1896, MO and *Small & West*, Aug. 1935, FLAS), and the specific epithet refers to Mr. J. M. Greenman who first recognized the distinctness of this taxon. It has been only little collected but is actually rather abundant in the wetlands within a very limited region of the Florida panhandle (Figure 1). Mathias and Constance (1942) noted that *O. filiformis* (Walter) Britton, a widespread coastal plain species extending from Florida northward to North Carolina and westward to Louisiana, was likely the closest relative of *O. greenmanii* Math. & Const. Both species have their leaves reduced to articulated (i.e., septated) phyllodes. Only the rare *O. canbyi* (Coult. & Rose) Fernald also possesses phyllodial leaves. However, this species has shorter phyllodial sheathes and fruits with thickened corky wings (see Mathias and Constance, 1949; Rodgers, 1950). Mathias and Constance (1942) reported that "In general, *O. Greenmanii* may be distinguished from *O. filiformis* by its greater stature, much larger phyllodes, more numerous rays and deep purple flowers." Godfrey and Kral (1958) also reported that "*Oxypolis greenmanii* is notably distinct from *O. filiformis* . . .". However, recent field investigations by the author and Kent D. Perkins have indicated extensive intergradation between these two taxa, and many intermediate populations are now known. Thus the taxonomic status of *O. greenmanii* is here reconsidered in connection with a study of the morphological, ecological, and geographical variability within this taxon and *O. filiformis*.

The range of morphological variation exhibited by *Oxypolis filiformis* and *O. greenmanii* was investigated throughout the geographical range of the two taxa, with special emphasis being given to (1) plant height, (2) basal phyllode size and shape, (3) prominence of phyllodial articulations, (4) number of primary rays per umbel, and (5) flower color, since these characters either had been used by earlier botanists in distinguishing these taxa or had been discovered to be particularly variable during preliminary field studies of the group. The pattern of variation in these (and other)

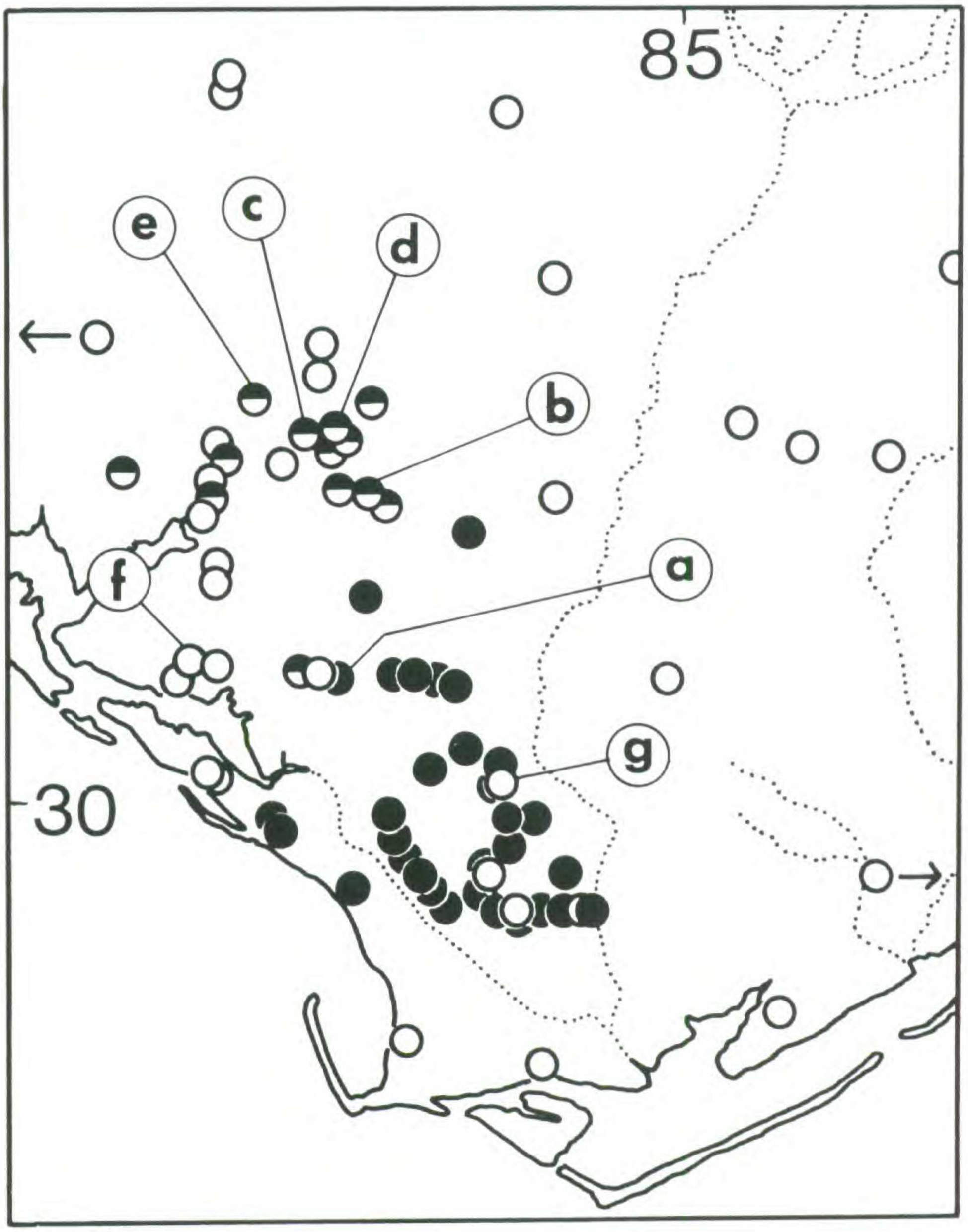


Figure 1. **Distribution of phyllodal-leaved Oxypolis in Gulf, Bay, and Calhoun counties, and in adjacent areas of Florida panhandle.** Open circle = population of *Oxypolis filiformis;* dot = population of *Oxypolis greenmanii;* half-shaded circle = intermediate population. For a presentation of morphological variability of labeled populations (a–g) see Figures 3–7 and discussion in text.

characters was determined through a study of herbarium specimens from throughout the range of the taxa, and by detailed field studies of seven populations of *Oxypolis* from Bay and Gulf counties, Florida.

Throughout most of its range *Oxypolis filiformis* was found to be characterized by individuals with at least slightly keeled and more or less obscurely articulated basal phyllodes and white flowers. In contrast, most individuals of *O. greenmanii* may be distinguished by their often larger and conspicuously articulated basal phyllodes that are round to elliptic in cross-section, i.e., not keeled, and deep to pale purple flowers (Figure 2). Great variation in height and

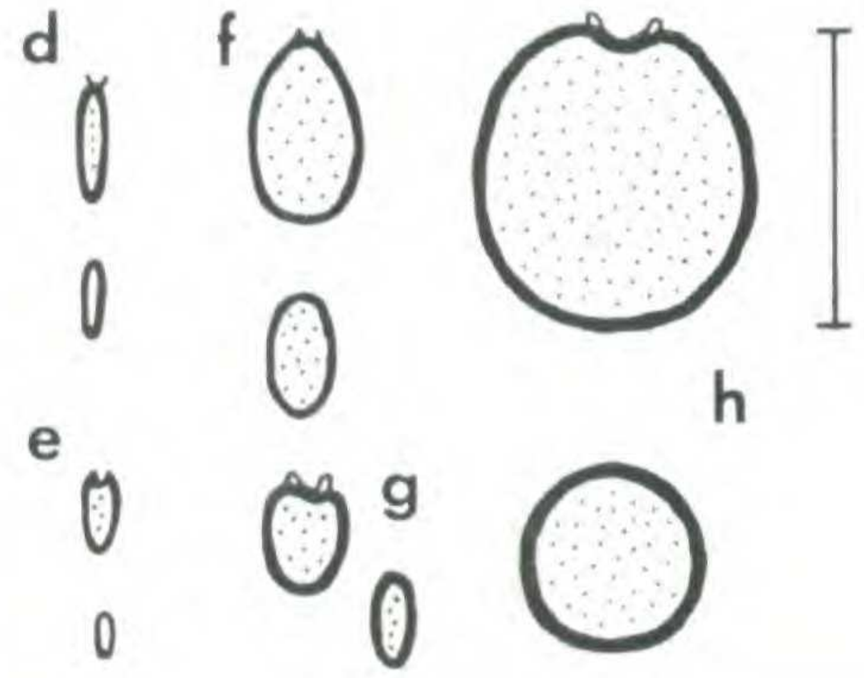
Table 1. **Variation in selected morphological characters in Oxypolis greenmanii and O. filiformis**

character	O. greenmanii	O. filiformis
Plant height	0.4–2.5 (−3) m	0.3–1.5(−2.5) m
Basal phyllode width[1]	ca. 4.5–17 mm	ca. 2–8 mm
Basal phyllode breadth[1]	ca. 4–17 mm	ca. 1–6 mm
Basal phyllode shape[1] (in cross-section)	round or elliptic, not keeled	flat and strongly keeled to elliptic and only slightly keeled
Phyllode articulations	± conspicuous	± inconspicuous
Flower color	deep to pale purple	white (to very slightly pink tinged)
Number of primary rays per umbel[2]	ca. 7–30	ca. 5–25

[1] Measured at apex of phyllode sheath; width = distance from adaxial to abaxial side of phyllode when cut in cross-section; breadth = distance across basal phyllode when cut in cross-section, i.e., perpendicular to width.

[2] Measured on largest umbel per plant (usually the terminal umbel).


a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"robustness" of plants exists in both taxa (Table 1). Similarly, the number of primary rays per umbel is extremely variable, and is thus of only very limited use in distinguishing the taxa (Table 1). (The use of both features by Mathias and Constance (1942, 1945) likely resulted from their very incomplete knowledge of the range of variability within this group.) It should also be noted here that flower color is not closely correlated with vegetative pigmentation; thus plants with deeply purple stems and phyllodes may have white flowers and vice versa. Populations referrable to *O. greenmanii* were found to be restricted to Gulf, Calhoun, and Bay counties, Florida. Such populations are most characteristic of *Hypericum* bogs (e.g., *Hypericum chapmanii, H. brachyphyllum, H. nitidum, H. fasciculatum*) but also occur in wet *Pinus elliottii* flatwoods, open *Taxodium ascendens* swamps, wet marshy areas, and disturbed roadside ditches. In contrast, *O. filiformis* is abundant throughout Florida. In the Florida panhandle this taxon was found to occur most frequently in sedge-grass-pitcher plant bogs or marshes and moist roadside ditches, but it can occur in wet *Pinus elliottii* flatwoods as well as *Taxodium ascendens* swamps. Within the region occupied by *O. greenmanii, O. filiformis* is rather uncommon and is mainly restricted to disturbed habitats along roadsides. However, many morphologically intermediate and taxonomically puzzling populations of *Oxypolis* were discovered in the northeastern portion of Bay County and in adjacent areas of Gulf County (Figure 1). These populations occur in both grass-sedge marshes and *Hypericum* bogs. This region marks the extreme northwestern extent of the range of *O. greenmanii,* and is characterized by many morphologically interesting *Oxypolis* populations, each of which is distinghished by a more or less distinctive character combination (i.e., genetic composition). Populations occur which are composed exclusively of plants that have robust, unkeeled basal phyllodes and white flowers. Other populations are composed of uniformly unkeeled plants which vary in flower color from white to pink or

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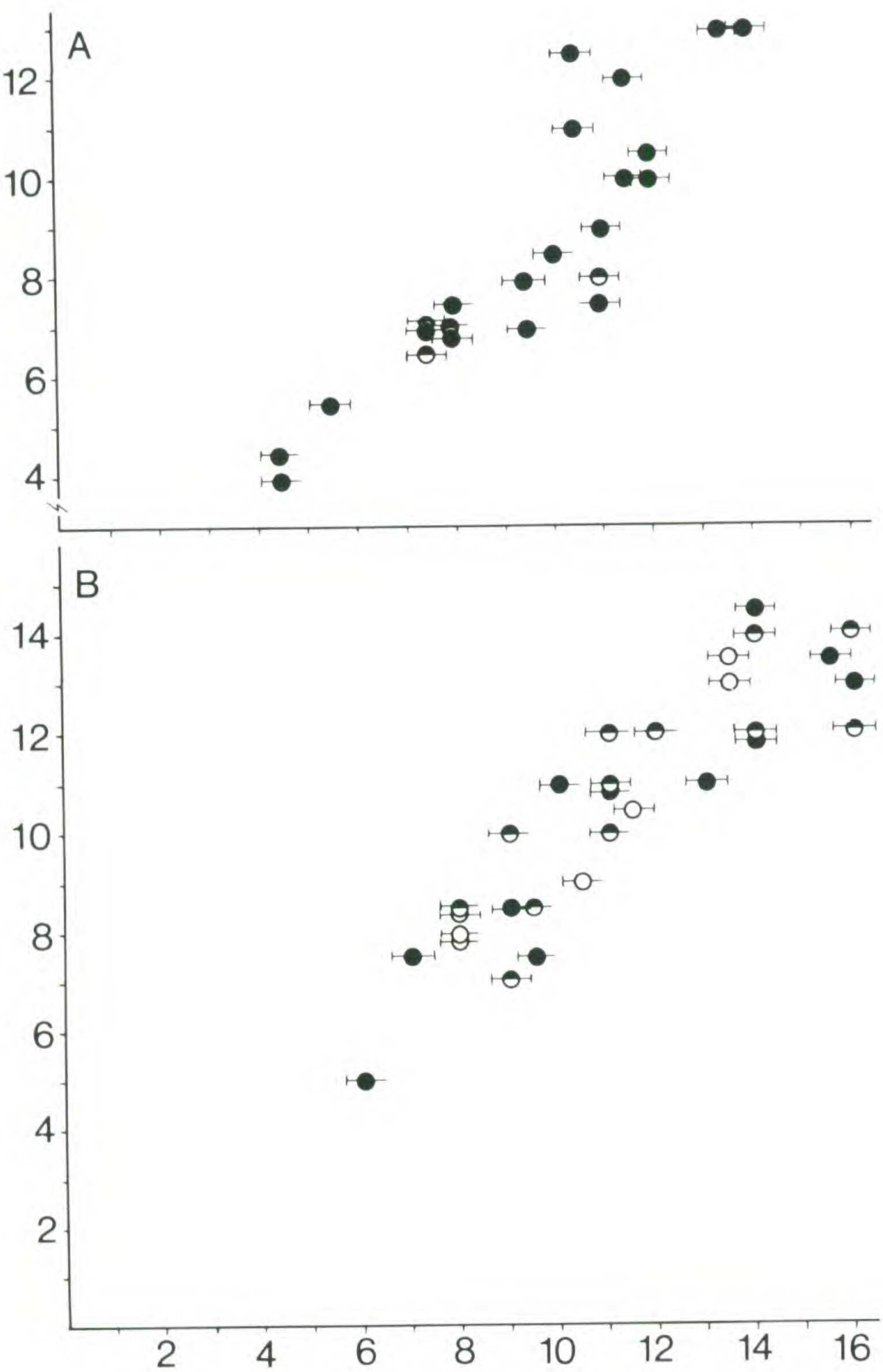
Figure 2. **Distinctive morphological characters of Oxypolis filiformis and O. greenmanii. a,** basal phyllodes of *O. greenmanii;* **b,c,** basal phyllodes of *O. filiformis.* **d–h,** cross-sections of basal phyllodes at apex of sheath, and midway between sheath and phyllode apex, scale = 15 mm: **d,e,** *O. filiformis;* **f,g,** intermediate plants; **h,** *O. greenmanii.* **i,j,** flowers: **i,** *O. filiformis* (white); **j,** *O. greenmanii* (purple).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purple, while still others are uniform in flower color but vary in the size and shape (in cross-section) of the basal phyllodes (see Figures 3–5). These populations completely bridge the morphological gap between *O. filiformis* and *O. greenmanii* as traditionally delimited. Four of these intermediate populations (indicated in Figure 1) were studied in detail in the field by recording information on flower color, and on size (both width and breadth), prominence of keel development, and conspicuousness of articulations of the basal phyllodes on ca. 15–30 individuals per population. Data were recorded in the field since all vegetative characters listed above are either destroyed or seriously distorted in pressed and dried specimens. In addition, specimen drying somewhat obscures flower color. However, voucher specimens were made from each population. Two additional populations were similarly studied—one of *O. greenmanii* from a region removed from populations of *O. filiformis*, and one of *O. filiformis* geographically distant from any population of *O. greenmanii*. These populations served as "standards" or indicators of the morphological variability in typical populations of both taxa.

The results of these field investigations are presented in Figures 3–5. These scatter diagrams clearly demonstrate the distinctive morphological composition of each population. They also indicate that some populations tend toward *O. filiformis* and others toward *O. greenmanii*. It is easily seen that the degree to which a population

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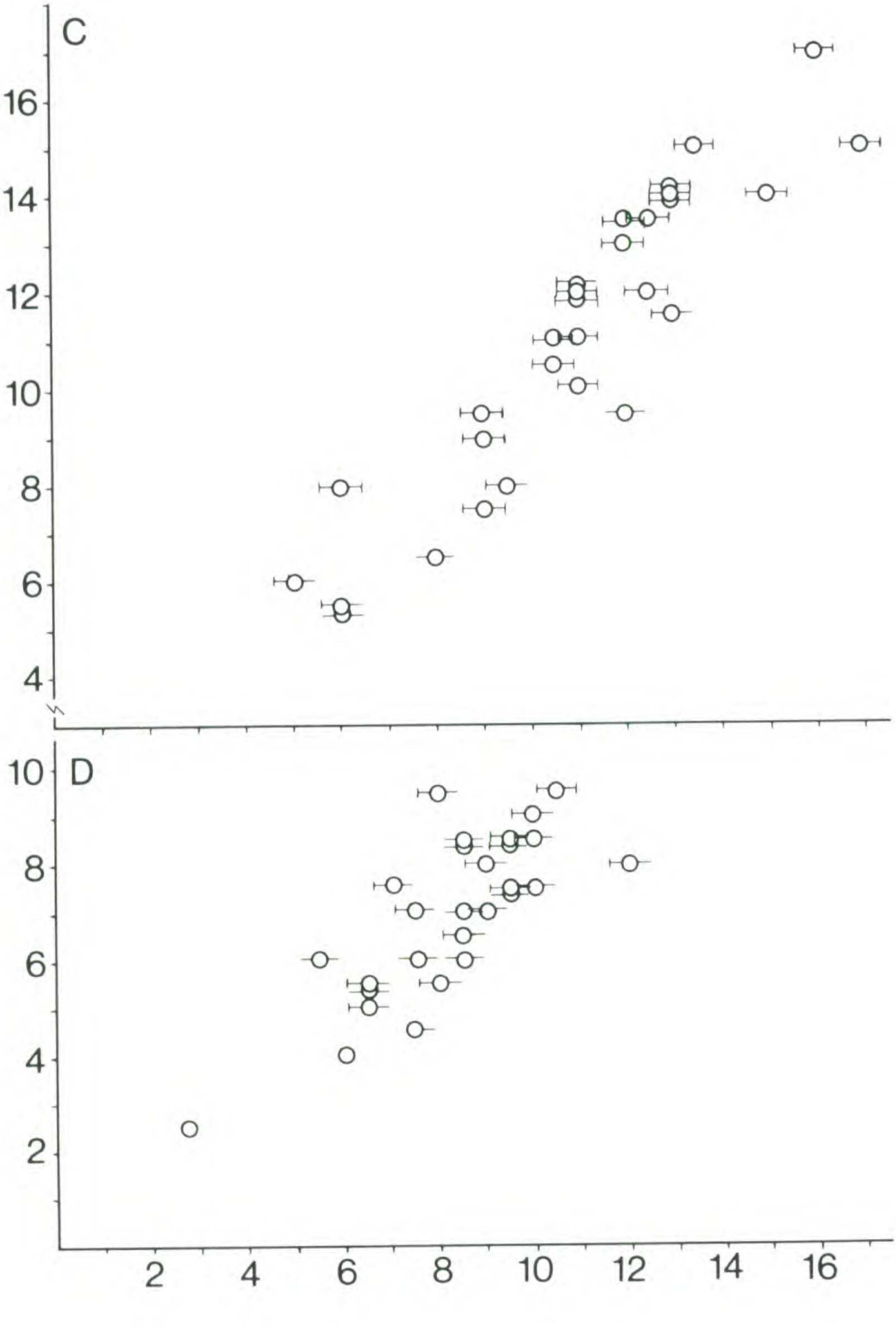
Figure 3. **Variation in certain morphological characters within selected Oxypolis populations of Gulf, Bay, and Calhoun counties, Florida.** Open circle = white flowered plant; half-shaded circle = ± pink flowered plant; dot = purple flowered plant. Full tail to left = basal phyllodes not keeled; half tail to left = phyllodes slightly keeled; no tail to left = phyllodes keeled. Full tail to right = phyllode articulations conspicuous and impressed; half tail to right = articulations inconspicuous; no tail to right = articulations slightly visible and raised. Horizontal axis = width of basal phyllodes in mm (i.e., distance from adaxial to abaxial side of phyllode when cut in cross-section at apex of sheath). Vertical axis = breadth of basal phyllodes in mm (i.e., distance across basal phyllode when cut in cross-section; perpendicular to width).

A. *Oxypolis greenmanii* population; Gulf Co., along Rt. 22, ca. 0.9 mi. E of Gulf/Bay County line, S18, T4S, R11W, in *Hypericum chapmanii* bog (with *H. brachyphyllum*) *Judd & Perkins 2321* (FLAS). **B.** Intermediate population; Calhoun Co., along Scotts Ferry Rd. ca. 4.5 mi. E of jct. with Rt. 231, S5, T2S, R11W, in *Hypericum fasciculatum* bog, *Judd & Perkins 2729* (FLAS).

For further information see Figure 1 and discussion in text.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resembles "standard" *O. greenmanii* is roughly correlated with its geographical distance from the Gulf-Calhoun-Bay county area in which this taxon occurs. Thus population "E" is morphologically closest to "standard" *O. filiformis* while population "B" is closest to *O. greenmanii* (see Figures 1, 3, and 5). If the "key" characters of the basal phyllodes and flowers are applied to the individuals composing these populations, some, i.e., "E" and "D", are seen to be composed of plants falling within the variation range of *O. filiformis* along with intermediate individuals, i.e., plants with white flowers and unkeeled or only very slightly keeled basal phyllodes, while population "B" is composed of plants falling within the range of variation of *O. greenmanii* along with intermediate individuals, in this case, white to pink flowered plants with more or less unkeeled basal phyllodes. Population "C" is composed of exclusively intermediate plants which possess the white flowers characteristic of *O. filiformis* and the large, unkeeled basal phyllodes characteristic of *O. greenmanii*! (See Figure 4). The morphological gap between *O. greenmanii* and *O. filiformis* is completely bridged using only these populations. However, many other similar intermediate populations exist within this area, resulting in a total morphological continuum between the two taxa (Figure 6).

It is important to note that the sets of characters usually distinguishing these two taxa are not correlated within these populations. Thus plants with robust, unkeeled basal phyllodes and white flowers are common, and within a population the plants with smaller phyllodes are not necessarily more frequently white flowered. Plants with slightly keeled leaves and purple flowers also occur. Although these intermediate populations show variation in characteristics that are usually invariant within most populations of either *O. filiformis* or *O. greenmanii,* they are not extremely

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Figure 4. **Variation in certain morphological characters within selected Oxypolis populations in Gulf, Bay, and Calhoun counties, Florida.** For explanation of symbols and graph axes see Figure 3.
C. Intermediate population; Bay Co., along Rt. 231, 1.8 mi. N of jct. with Rt. 388 (N of Youngstown), S15, T1S, R12W, in *Hypericum fasciculatum* swamp, *Judd & Perkins 2400–2405, 2714* (selected specimens at FLAS).
D. Intermediate population; Bay Co., along Linger-Longer Rd. ca. 1.4 mi. E of jct. with Rt. 231, S14, T1S, R12W, in grass-sedge marsh at edge of pinelands with *Sarracenia* and *Cyrilla, Judd & Perkins 2718* (FLAS).
For further information see Figure 1 and discussion in text.

variable, that is, such populations are *not* composed of individuals referrable to typical *O. greenmanii* and *O. filiformis* along with a host of intermediate plants. Rather, as described above, the populations exhibit a range of morphological variation comparable with that of "standard" populations of both taxa (compare Figures 3-5). These populations are, in fact, often uniformly intermediate in

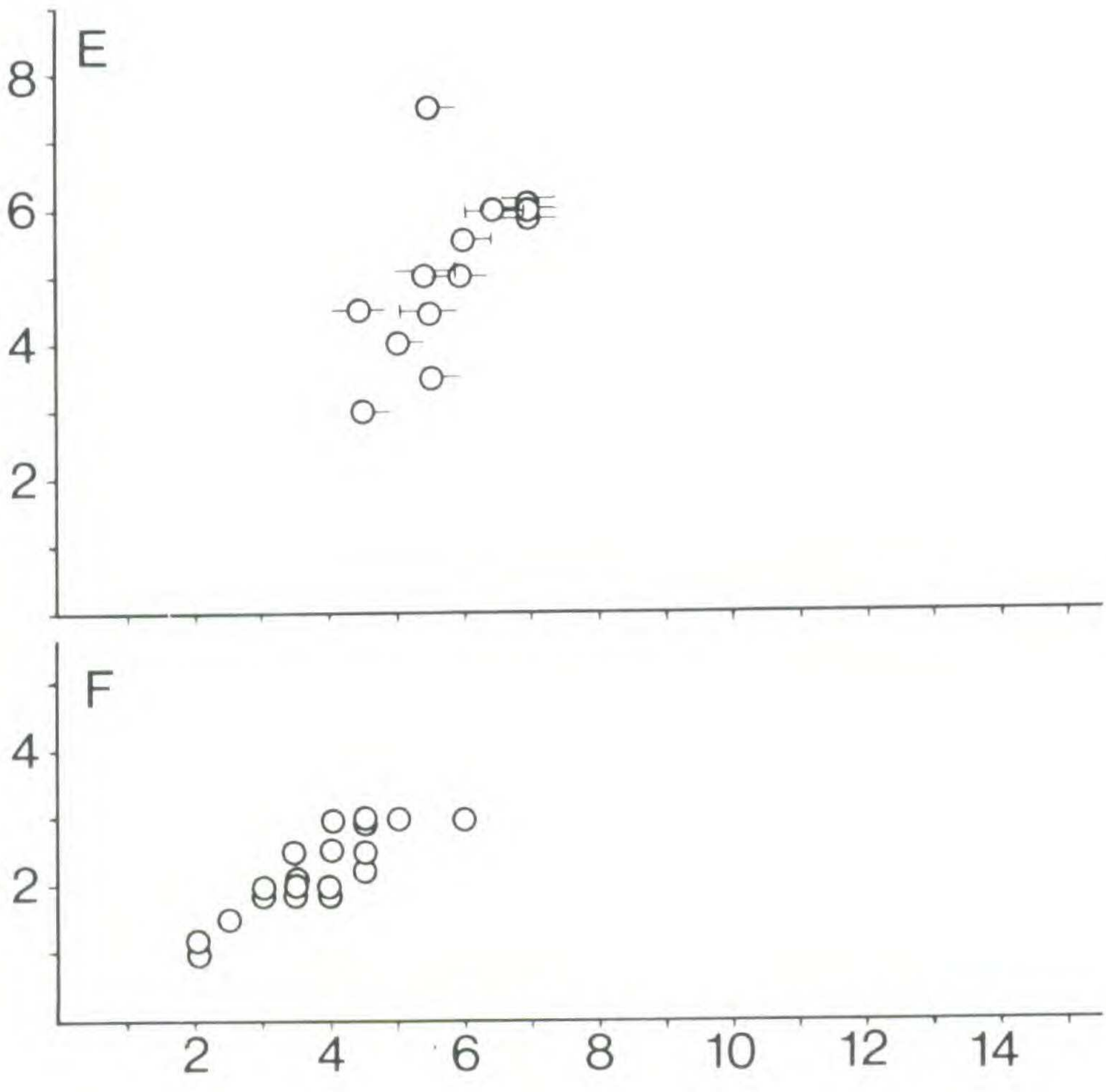

Figure 5. **Variation in certain morphological characters within selected Oxypolis populations in Gulf, Bay, and Calhoun counties, Florida.** For explanation of symbols and graph axes see Figure 3.
E. Intermediate population; Bay/Washington County line, along Rt. 20, 2.8 mi. E of Econfina Creek, S1, T1S, R13W, in *Hypericum fasciculatum* bog, *Judd & Perkins 2738* (FLAS).
F. *Oxypolis filiformis* population; Bay Co., jct. of Callaway Bayou and Rt. 22, S9, T4S, R13W, *Judd & Perkins 2428-2432* (selected specimens at FLAS).
For further information see Figure 1 and discussion in text.

several characters (see scatter diagram of population "C" in Figure 4) and may therefore be placed at definite locations along a continuum of variation connecting typical *O. greenmanii* with typical *O. filiformis*. All individuals in the studied populations were flowering and fruiting vigorously and all plants tested were found to be highly fertile (ca. 90% to nearly all pollen grains stained with cotton-blue in lacto-phenol). Such evidence would seem to discount the possibility of a hybrid origin for these populations.

However, many extremely variable *Oxypolis* populations do exist within the geographic range of *O. greenmanii* (see Figures 1 and 7). These populations, unlike those discussed above, are limited to disturbed wet roadside habitats, and are extremely variable, being composed of typical *O. filiformis* and *O. greenmanii* along with a nearly complete selection of intermediate plants. Within these populations there is a clear correlation between degree of keeling, size of basal phyllodes, and flower color (Figure 7). The variation pattern of such populations is probably best explained as a result of the crossing of plants occupying the extremes of the morphological continuum described above. Most of the presumed hybrid plants composing these variable populations are highly fertile (ca. 90% to nearly all pollen grains stained with cotton-blue in lacto-phenol), however, one had only ca. 50% stained grains. All plants falling within the variation range of either *O. greenmanii* or *O. filiformis* are very fertile (ca. 95% to nearly all grains stained). Both *O. greenmanii* and *O. filiformis* have a chromosome number of $n = 14$ (Bell & Constance, 1957, 1960), flower together, and seem not to be isolated by cytological or seasonal factors. Pollinator differences may lead to partial isolation since the white flowers of *O. filiformis* are visited by many unspecialized insects, while the purple flowers of *O. greenmanii* are visited mainly by various wasps (see Lindsey & Bell, 1981). However, we noted both tuphiid and vespid wasps (*Myzinum* and *Polistes*) visiting the flowers of both taxa and the effectiveness of this isolating mechanism is called into question by the many "hybrid" populations in existence.

It is evident from the data presented above that *Oxypolis greenmanii* can no longer be maintained as a distinct species, but should instead be considered a subspecies of the widespread *O. filiformis*. This taxonomic change is necessitated because the two taxa are evidently completely interfertile (breeding studies would be valuable here) and are connected by an extensive series of

intermediate populations. The most useful characters in distinguishing the subspecies are flower color (purple in ssp. *greenmanii vs.* white in ssp. *filiformis*) and basal phyllode morphology (± large, unkeeled, and conspicuously articulated in ssp. *greenmanii vs.* smaller, » keeled, and inconspicuously articulated in ssp. *filiformis*). Living (or liquid-preserved) material is required for positive identification (especially of fruiting material) since all known taxonomically useful characters of the basal phyllodes are either destroyed or seriously distorted during pressing and drying.

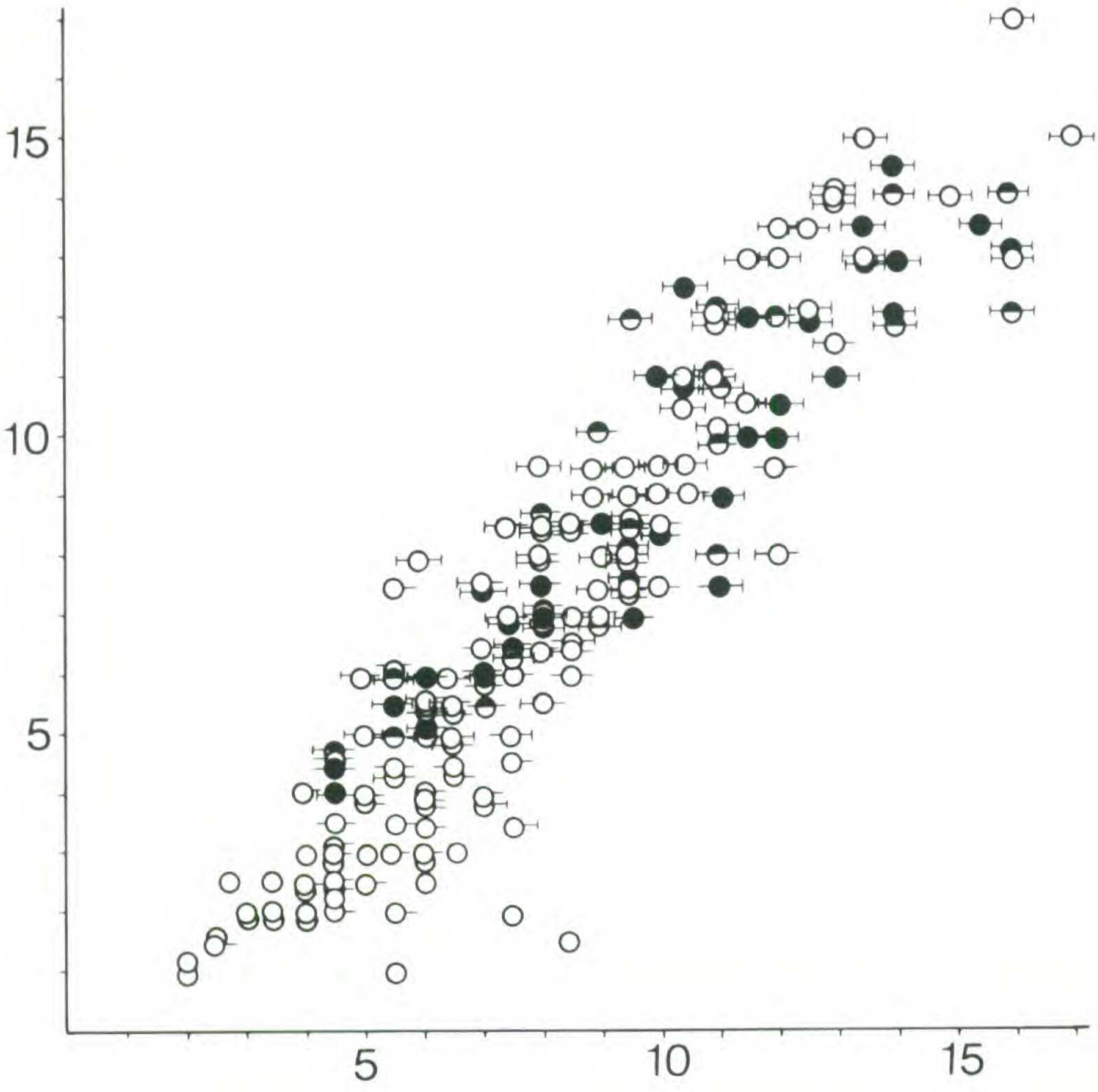

Figure 6. **Variation in certain morphological characters within field-sampled populations of Oxypolis filiformis and O. greenmanii within Gulf, Bay, and Calhoun counties, and adjacent regions of the Florida panhandle.** (Obviously "hybrid" populations have been excluded.) See Figure 3 for explanation of symbols and graph axes.

Oxypolis filiformis (Walter) Britton ssp. **greenmanii** (Math. & Const.) Judd, *comb. et stat. nov.* (*Oxypolis greenmanii* Math. & Const. Bull. Torrey Bot. Club **62**: 152. 1942.)

REPRESENTATIVE SPECIMENS: UNITED STATES, **Florida.** BAY CO.: ca. 1 mi. E of Rd. to Baker Point & 1 mi. N of U. S. 98, Tyndall Air Force Base, S5, T6S, R12W, *Judd & Perkins 2440* (FLAS); Fla. 22, 5.2 mi. E of jct. with Rt. 167, S14, T4S, R12W, *Judd and Perkins 2741* (FLAS). CALHOUN CO.: 1.4 mi. N of jct. of Fla. 73 & Rt. C-392, ca. 3 mi. N of Kinard, S15, T2S, R10W, *Judd & Perkins 2390* (FLAS); Scotts Ferry Rd., ca. 4.5 mi. E of jct. with U. S. 231, S5, T2S, R11W, *Judd & Perkins 2729d* (FLAS); 12 mi. W of Wewahitchka (Tenmile Swamp Quad), T3S, R11W, *McDaniel 5721* (FSU). GULF CO.: Fla. 71, 13–14 mi. N of Port St. Joe, *Godfrey & Jervis 53690* (FSU); White City Rd., 2.6 mi. S of jct. with Fla. 381, S14, T6S, R9W, *Judd & Perkins 2328* (FLAS); just W of Howard Creek Subdivision, S1, T7S, R9W, *Judd & Perkins 2348* (FLAS); ca. 1 mi. N of jct. of Rt. 381-A & Fla. 71, ca. 6 mi. S of Wewahitchka, S30, T5S, R9W, *Judd & Perkins 2368* (FLAS); Rd. 20, 4 mi. SE of Overstreet, S14, T6S, R11W, *Judd & Perkins 2379* (FLAS); 4.5 mi. NE of Early, *Thorne 17317* (FLAS, FSU).

Oxypolis filiformis subspecies *filiformis* and *greenmanii* are probably isolated by a combination of ethological (pollinator differences), ecological, and geographical factors, with ssp. *filiformis* being essentially replaced in the wetland habitats of Gulf county by ssp. *greenmanii*, with ssp. *greenmanii* occurring mainly in *Hypericum* bog habitats *vs.* grass-sedge marsh habitats for ssp. *filiformis*, and with the two subspecies differing in flower color (and thus attracting a somewhat different pollinator spectrum—see Lindsey and Bell, 1981). It is of interest that the morphologically intermediate populations are adjacent to and partially overlap the northwestern portion of the range of ssp. *greenmanii*. It is possible that ssp. *greenmanii* diverged both morphologically (in floral and vegetative features) and ecologically as its ancestors migrated into the Gulf County region from adjacent northern areas, thus forming this cline-like series of intermediate populations. However, this variation pattern may have been produced through past hybridization and introgression between two previously isolated populations. In contrast, the extremely variable "hybrid" populations likely

result from a more recent spread of ssp. *filiformis* into this region following the construction of roads and highways (and the associated increase in disturbed, open, wet, grassy habitats). As *O. filiformis* ssp. *filiformis* spread into this region it encountered ssp. *greenmanii* (which is abundant in *Hypericum* bogs which can be found adjacent to highways). Both subspecies colonized the disturbed roadside habitats and interbreeding occurred. The fascinating variability of *Oxypolis filiformis* in the Florida panhandle thus may be explained through a combination of both primary (gradual geographical intergradation) and secondary (recent hybridization) factors (see Mayr, 1969).

Oxypolis filiformis ssp. *greenmanii* is one of several taxa endemic to various low-elevation habitats of the Florida panhandle, e.g., *Macbridea alba, Rudbeckia graminifolia, Hypericum lissophloeus,*

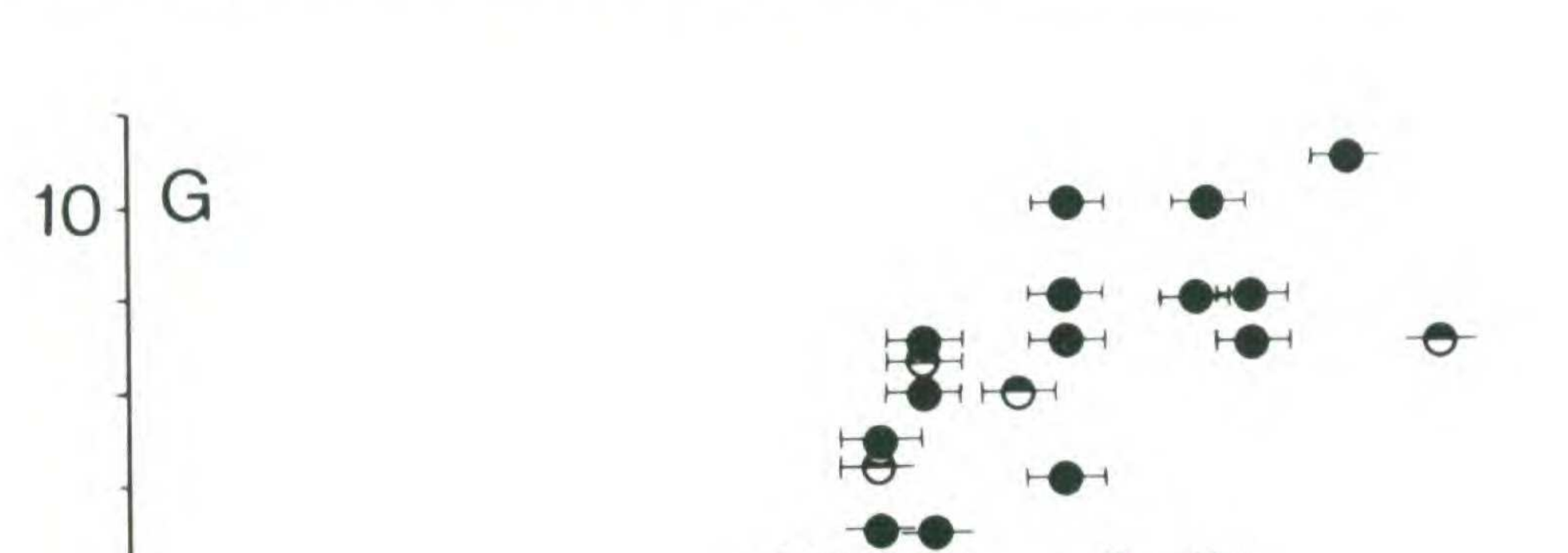

Figure 7. **Variation in certain morphological characters within population "G"—an extremely variable population consisting of Oxypolis filiformis, O. greenmanii and presumed hybrids.** Gulf Co., along Rt. 71, ca. 4 mi. S of jct. with Rt. 22 (S of Wewahitchka), in wet, disturbed roadside ditch, *Judd & Perkins 2749* (FLAS). See Figure 3 for explanation of symbols and graph axes.

Hypericum chapmanii, Gentiana pennelliana, Hedeoma graveolens, Liatris provincialis, Verbesina chapmanii, and *Xyris longisepala* (see also Ward, 1979). The causes of this area's high degree of endemism are poorly understood, but may eventually be clarified through systematic studies of the region's endemics.

ACKNOWLEDGMENTS

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